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A. MADREPORARIA EXCLUDING FLABELLIDÆ AND TURBINOLIDÆ

BY
J. STANLEY GARDINER, F.R.S., AND PEGGY WAUGH

B. THE ECOLOGY OF SOLITARY CORALS

BY
J. STANLEY GARDINER, M.A., F.R.S.

WITH TWO PLATES AND THREE TEXT-FIGURES

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THE Flabellidæ and Turbinolidæ were reported on by us in Vol. V of this series, pp. 168–202 (1938); they were assigned to 14 genera and 33 species were determined. The present report deals with the rest of the Madreporaria and concerns 16 genera and 36 species, making a total of 30 genera and 69 species.

The collection is of importance in that there is an abundance of specimens of a few species and a fair series of many, these often collected from several dredgings. Such sets allow a study of the environmental variation in their species and a determination as to the characters which are to be regarded as specific. Where they exist, we have compared our species with the type specimens in the British Museum, where Moseley's and Duncan's coralla may be found and to which sets from the present collection are being now added, as well as the species dealt with in the Reports of the Percy Sladen Expedition to the Indian Ocean, together with those of the Maldive and Laccadive Expedition. We have also greatly benefited by a set of co-types of many of Pourtalès, dredged species from the West Indies most generously sent to us by Dr. Thomas Barbour, the enlightened Director of the Agassiz Museum; these also will be found in the British Museum.

The technique we have adopted has been independent determinations of what corals are species and then a joint consideration, followed by a tabulation of their supposed specific characters. Then followed the search of literature to determine genera and species. This has been materially helped by the fact the senior of us has discussed many species and taxonomic questions with workers on the collections of several modern expeditions, while both of us have examined corals when growing on reefs. We have not generally attempted lists of synonyms. Inadequately described corals—and most named on one or two specimens may be so characterized—had better disappear from literature altogether than be forced under some species to which they have often no relation. This is especially the case with young forms, growth incomplete, such resembling each other in any genus more closely than do the adults.

Family Oculinidæ.

Genus *Madrepora* Linnæus.

(*Vide*, Vaughan, ' U.S. Nat. Mus.,' Bull. 59, 80 [1907]).

Obeying the laws of nomenclature we have to employ the above generic name in place of either *Lophelia*, *Amphelia* or *Diphelia*, all Ed. & H. For unstated reasons Vaughan preferred *M. oculata* as the genotype, the other possible species being *M. prolifera*, the two species subsequently separated by Ed. & H. as representing respectively the genera *Amphelia* and *Lophelia*. Duncan* agreed, distinguishing *Lophelia* by the presence of dissepimental tissues and perhaps tabulæ and the absence of a columella, but he assigned *Diphelia* to this genus.

In the growth-form all three genera agree, and certainly, in a series of our specimens of *M. oculata* from off the west coast of Ireland, there are no conspicuous dissepiments, and the corallite cavities are sometimes completely obliterated, as Vaughan stated, by a secondary deposition of corallum. The inner edges of the larger septa always fuse, and there may arise upon this fusion upstanding pillars forming a pseudo-columella ; thus there is always a shallow calice. Pending further knowledge, including a comparison between the polyps of *M. prolifera* and *M. oculata*, we accept Vaughan's designation of the genus—a course which further appeals when many species are examined. This we were enabled to do, as the British Museum loaned to us their collection, which included not only Moseley's types from the " Challenger ", but miscellaneous specimens of kindred genera and a large collection of *M. prolifera*, of which a special study was made so as to determine the variation of the species. Curiously enough, *M. oculata* was not represented, but we have been able to add a series to the British Museum collection.

Of Moseley's " Challenger " types *arbuscula* was dead, its surface obviously so greatly altered that the description is almost valueless. Unfortunately Alcock† did not help us, his only addition being the statement " no costæ, cœnenchyma dense and very smooth ".

Moseley's *tenuis* depended on a fragment, which might quite well belong to *M. infundibulifera* Duncan,‡ the type of which we are unable to find. We are inclined to regard Moseley's *candida* as a good species, but three additional boxes in the British Museum suggest a wide variation almost parallel to *M. prolifera*. *M. investigatoris* Alcock§ and *exigua* Pourtalès|| judging by the specimens before us must be accepted, but *carolina*|| can never be determined from Pourtalès' description and Alcock's *moresbyi*§ scarcely seems to us beyond the limits of variation of *investigatoris* and other species.

Madrepora ramea (Duncan).

Trans. Zool. Soc. VIII, 326, xlvi (1873).

Pieces of two colonies from St. 157, 229 m., coral and rock, would seem to fall within the variation of this species, Duncan's figures of which are admirable in some ways, while his description is so scanty that an account of our specimens may be helpful.

* ' Trans. Zool. Soc.' VIII, 234 (1873).
† ' " Siboga " Exp.' 34 (1902).
‡ ' Proc. Zool. Soc.' 1871, 276, xxiv, 4.
§ ' " Investigator " Rep.' 25, iii, 1 (1898).
|| ' Cat. Mus. Comp. Zool.' 26, i, 6–7 (1871).

Corallum branches irregularly, but the pieces before us suggest horizontal spreading, the upper sides alone with corallites, whose edges rise for only ·5 to 2 cm. above the general level of the stems. The calices vary up to 4 mm. in diameter, the terminal about half this size.

There is a thick deposition of corallum externally and the central connections of the calices may be largely filled by a similar deposition internally.

The species closely resembles *kauaiensis* in its granular surface and in its coarse longitudinal striæ, these being continuous along the whole under surface. Some of these on the upper surface are associated with septa and are costal, but around each calice the lines are obscured and twisted, in some parts with an almost perforate appearance. The striæ show best on the older and larger parts of the corallum and are often strengthened by transverse bars.

The septa are in three cycles, in larger calices with a few of a fourth cycle. The septal margins are toothed, and the septa are little exsert. Not less than 12 septa are joined by trabeculæ from their inner ends, thus forming a columella the papillæ on which may merge externally with the septal teeth.

Madrepora kauaiensis Vaughan.

Vaughan, U.S. Nat. Mus., Bull. 59, 81, viii, 1, 2, (1907).

The above excellent description applied equally well to our specimens, the sole difference being that our calices are, as a rule, not " solidly filled with stereoplasm ", the cavity persisting as is usually the case in *M. oculata* and *prolifera*. Even in filled-up cavities of *oculata* we find that the position of the original cavity is usually to be recognized by a slight difference in colour and texture of the corallum as compared to the very dense and often thick corallum surrounding the same.

St. 42, 1415 m., r. m., dead ; St. 108, 786 m., gy. m., dead material with some living branches ; St. 122, 732 m., gy. gr. m., as last, the dead coral near the base of colonies with central worm tubes ; St. 124, 914 m., gy. gr. m. s., a fragment growing on a stem formed of elongated sponge spicules ; St. 184, 1270 m., gn. m., dead.

Madrepora investigatoris Alcock.

" Investigator " Rep., 24, iii, 1*a–b* (1898).

Dead material from St. 42, 1415 m., r. m., St. 54, 952 m., 1046 m., gn. m., and St. 184, 1270 m., gn. m., contains coralla of this species. There are also fragments of a species with larger corallites, which cannot be identified.

Growth-variation in *M. prolifera* (Linnæus).

Among deep-sea corals, viz. living below the light zone, Duncan* has already referred to the great variation of this species. The start is a simple polyp, from which a secondary polyp is given off close below its tentacles ; its cavity remains continuous with that of its parent, at least for a long period, but its internal corallum is laid on to that of its parent.

* ' Trans. Zool. Soc.' VIII, 303 (1873).

A third polyp is budded out from the second polyp, but on the opposite side of the stem—and so on ; the result is a zig-zag stem with a polyp standing up at every angle. Externally, the whole corallum is covered by polyp-tissues, which are continuously depositing further corallum on the skeleton below them. Internally there is the small central connection of the polyps along the stem, into which 12 to 24 septa project, its diameter dependent on that of the original bud. This is not immediately reduced by deposition of corallum, being only completely closed towards the bases of heavy colonies. Its septa, however, are joined across by irregularly-arranged trabeculæ, especially towards the centre of the tube. While these may completely close the internal connections of polyps, we have failed in this type of growth to find the horizontal tabulæ of Duncan, which are supposed to act to this end. The corallites rarely possess more than 48 septa, and these are usually rather irregularly arranged, 6 to 12 markedly more exsert. The septa are untoothed, and pali and columella are not found, though the septa may unite in the centre of the calice. The costæ of the larger septa exist until the valleys between them are filled by deposition of corallum.

In a collection of corals of this species the typical growth-form as sketched above may be scarcely recognizable, the mode only visible at the ends of branches. Additional buds may form on the surface half-way down polyps, and from these new stems may grow out, giving rise to a mass of branches which fuse wherever polyp tissues touch. Where there is open water and a firm base of attachment (as in an example from a telegraph cable), the coral grows up for a few inches and then spreads horizontally. Most specimens from the coasts of the North Atlantic show this to some degree, one from Lousy Bank being so extreme as to suggest current influence in addition. On such horizontal growths it is noticeable that there is no absence of polyps in their under-surfaces, their number only showing reduction, which is sometimes compensated for by increased size.

Instead of the terminal polyp giving off a single bud, there may be a pair opposite one another, when two stems will be formed with an axillary polyp between. In place of a pair there may be three or more buds irregularly arranged or perhaps on the same side. As already mentioned, polyps may be budded off from the sides of older polyps, their corallites unconnected with the central cavities of the parent stem, but this is not usual. This phenomenon is best seen in a colony from Portuguese waters, where the polyps are all striving to grow in a single direction, presumably at right angles to the attachment of their colony. The result is a multiplicity of tightly-packed stems, ending in elongated vertically-growing polyps.* The coral stems show little thickening and, in consequence, the costæ of the larger septa may extend for 1 or 2 cm. down the outsides of the branches.† Internally in these elongated corallites dissepiments are more regular and may simulate tabulæ.

In normal colonies there are great differences in the size and massiveness of the stems produced by the external deposition of corallum. The corallites also vary greatly in size, in one colony having an average diameter twice that of another ; usually a few giant corallites of 10 to 12 mm. diameter are found in any large colony. A stem may be so thickened that there are no costæ, and corallites, once standing up freely, may appear sessile. The larger septa may be scarcely exsert at all, but generally 12 septa stand up

* We may deduce that this coral was growing in a hole, or on a very soft bottom, into which its weight was causing sinkage.

† Compare *M. anthrophyllites* E. & S. [Ed. & H., ' Cor.' II, 118].

for 2 to 3 mm. in a characteristic manner. Beyond 24 the number of septa depends on the size and shape, especially the compression, of each individual corallite.

Lastly, there is the association of this coral with *Eunice*. The polyp tissues may grow over and around shells and other foreign objects, with which they come into contact, so as completely to imbed them. This is presumably the case with this worm, but the process is not clear. The final effect is that about half the colonies have hollow stems, in which cavities *Eunice* dwells. It certainly did not bore these, and the association is one requiring study. It is found also in *M. oculata*, particularly abundantly off the coasts of the North Atlantic.

Genus *Madracis* Ed. & H.

We have before us the following specimens from the Indian Ocean. We deem them to be too small and few for identification.

(*a*) " Murray " St. 67, 274 m., sft. gn. m. st., a broken-off branch, dead and much worn, the facies of *M. asperula* Ed. & H.

(*b*) " Murray " St. 111, 73–165 m., ? r., a small incrustation with about 25 tightly-packed calices not exceeding 2 mm. in diameter, 10 large septa and 10 others, calicular appearance recalling *M. kauaiensis* Vaughan (Bull. 59, ' U.S. Nat. Mus.', 83, ix, 1907).

(*c*) " Murray " St. 149, 311–339 m., c. s. sh. cr., a dead colony with branches, resembling *M. hellana* Ed. & H.

(*d*) " Maldive " Expedition, Kolumadulu 2, 30–35 fms., a small encrusting mass and an upstanding pillar, resembling the Mediterranean species *M. pharensis* Döderlein (' Mitt. Zool. Sta. Neapel,' XXI, 183, 1913).

(*e*) " Sealark " Expedition, off Salomon Atoll, Chagos, 60–120 fms., a small incrusting mass, which may belong to *M. decactis* Lyman (' Proc. Boston Soc. Nat. Hist.', VI, 1867, and Pourtalès, ' Cat. Mus. Comp. Zool.', IV, 28, 1871).

Genus *Parasmilia* Ed. & H.

Parasmilia fecunda Pourtalès.

Cœlosmilia fecunda Pourtalès, Cat. Mus. Comp. Zool. IV, 21, p. 6, i, 12 ; iii, 4, 5, ; vi, 14, 15 (1871).
Parasmilia fecunda Lindström, Kongl. Svensk. Akad., 21 (1877) ; Marenzeller, " Valdivia " Exp., 311, xv, 5 (1904) ; Gravier, Comp. Sci., Monaco, LV, 91, xi, 169–73 (1920).

St. 209, 366 m., gr. br. m. r.

Five specimens belong to this species, which Marenzeller obtained off Sumatra, 380 m., previous records being from the West Indies and Atlantic. The cycles of septa are very distinct in thickness and there is a marked tendency, best seen in sections, for the septa of the latest cycle to converge on that which precedes it. Our specimens agree closely with those which Pourtalès described.

Genus *Solenosmilia* Duncan.

Solenosmilia variabilis Duncan.

Duncan, Trans. Zool. Soc. VIII, 327, xlii (1871) ; Moseley, " Challenger " Rep., 181, ix, 1–5 (1881) Gardiner, Trans. Roy. Soc., Edin. XLIX, 689 (1913).

St. 209, 366 m., gr. br. m. r.

There are 21 stems of this species, all dead but little decayed. They are all thickened

by extrathecal deposition of corallum, and this has presumably covered the costæ, except close under the calices, so that the stems are quite smooth.

The Scottish National Antarctic Expedition obtained this species in lat 37° 56′ N., long. 29° 11′ W. It seems to be generally distributed over the Atlantic into the Antarctic down to 1000 fms. Now its range is extended into the Indian Ocean. I have also a series, sent to me by the late Prof. Gilchrist, from off Natal ; they are quite indistinguishable from the present forms. *S. jeffreyi* Alcock may be identical, an " immense mass " from 434 fms., with larger calices, diagnosed by us as having existed in the happiest environment.

Genus *Culicia* Dana.

Cylicia Ed. & H., Cor. II, 606 (1857).

We have before us specimens which superficially might be assigned to five species ; they were collected in the Red Sea, Indian and Pacific Oceans. All the calices have the epitheca as their wall and a creeping, low growth. Their differences lie in variations of septa, pali and columella-rods and also to a certain degree in size and depths of calices, all of which characters show a wide range. The difficulty is to identify them with described species, for the range of variation of no species has been accurately determined.

Culicia tenella (Dana).

Dana, Zooph., 377, xxviii, 6 (1846).

St. 89, 135–183 m., s. sh. r., 2 small colonies ; St. 123, 256–366 m., gn. m. s. r., 2 small pieces.

These agree with the description above, but few corallites are undistorted, having been killed around their edges by the growth of other organisms. There tend to be present a few septa of cycle IV, but the cycles are not generally clear. The species appears to us to range from low tide to the above depth.

Genus *Fungia*.

The following material does not admit of specific identification. It is all of the *patella*-type, which was reconsidered in a special " Siboga " Expedition Report in 1923 by Dr. Boschma.

St. 103, 101 m., c. s. sp., 1 piece *Diaseris*-form, dead ; St. 106, 183–194 m., gr. m., 2 dead ; St. 126, 209 m., lt. br. m. sp., 2 whole and 2 pieces, 1 with open scar of attachment, recently dead ; St. 141, 44 m., c. s. sh. cr., 15 pieces *Diaseris*-form, dead, 10 *Cyclo-seris*-form, mostly dead and young ; St. 144, 31 m., c. sh. s., 1 living and 2 dead ; St. 154, 457 m., 3 pieces *Diaseris*-form, dead ; St. 161, 46 m., c. s., 5 tiny specimens, mostly living.

Genus *Bathyactis* Moseley.

Bathyactis symmetrica (Pourtalès).

Fungia symmetrica Pourtalès, Cat. Mus. Comp. Zool. IV, 46, vii, 5, 6, (1871).
Bathyactis symmetrica Moseley, " Challenger " Rep., 186, xi, 1–13 (1881).

St. 185, 2000 m., gn. m., 7 flat discs with all parts thin and fragile ; they measure 28, 33, 15, 14, 12, 10 and 9 mm. across. Their lower sides have 12 costæ more prominent, radiating from a slightly upstanding, central point ; otherwise the plicate arrangement

is as described by Moseley. The largest specimen shows quinary septa in the only unbroken piece of its margin. The columella part is filled by twisted and anastomosing trabeculæ from septa I and II.

St. 176, 655–732 m., gn. m. s., part of a disc regenerating; St. 54, 1046 m., gr. m., a disc of 5 mm.

Bathyactis (*?*) *symmetrica* (Pourtalès).

St. 59, 1948 m., sft. gn. m. A single dead specimen, 8 mm. diameter, characterized by a firmer skeleton and regular margin; costæ in centre less marked owing to a secondary

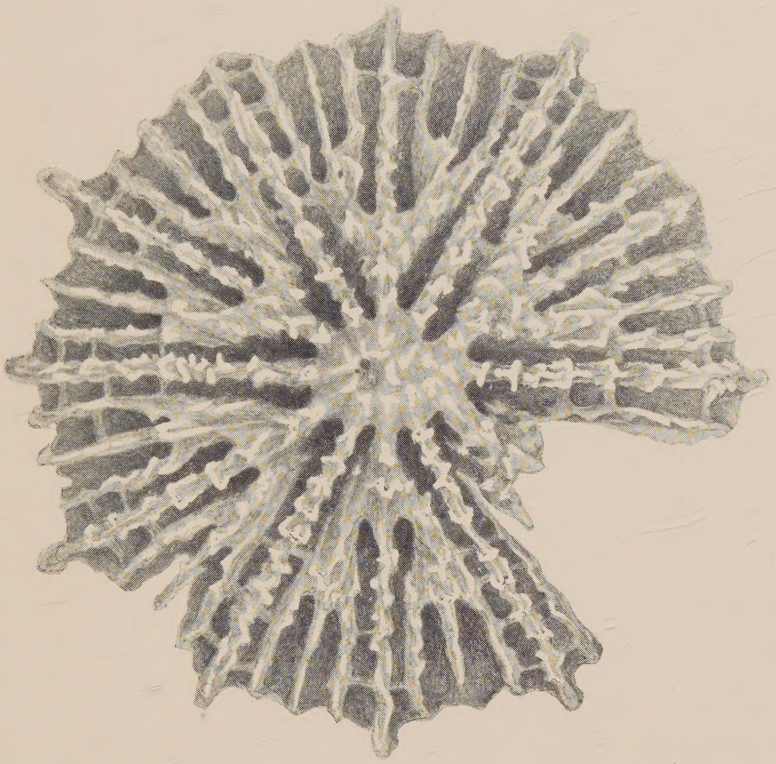

FIG. 1.—*Bathyactis stabilis* n. sp. Upper surface. × 10.

deposition of corallum; septa very regular, not nearly so high as in normal specimens of *symmetrica* of the same size; synapticulæ abundant but not in regular concentric circles; no pali and a rather solid junction of septa I and II in centre. These appearances may be due in part to a secondary deposition of lime after death.

Bathyactis stabilis n. sp. (Text-figs. 1 and 2.)

St. 118, 1789 m., gl. oz., a single specimen, 10 mm. across, one sector broken when obtained and regenerating.

Completely discoidal, with a rather firm skeleton. Basal wall flat, marked by 12 distinct costæ and 12 smaller intermediates, all reaching a prominent point in the centre, with 24 others alternating with these and not reaching the centre.

Septa, 4 complete cycles, 6 primaries free and the rest showing the typical, generic, deltoid characters. Septa all relatively low, straight (not wavy), toothed. Synapticulæ

very scarce, no circular arrangement, innermost about the level of the junction of septa IV to III.

Septa I and II slope down to the centre of the corallum, giving rise to a broad central columella-like fusion, on which arises a small central style with a ring of 12 similar rods around, as if derived from teeth on the inner ends of the larger septa, the whole rather irregular (*vide* Fig. 1).

This species closely resembles Moseley's pl. xi, fig. 10, of *Bathyactis symmetrica* ; this clearly is not a growth stage and may be our *Bathyactis stabilis*.

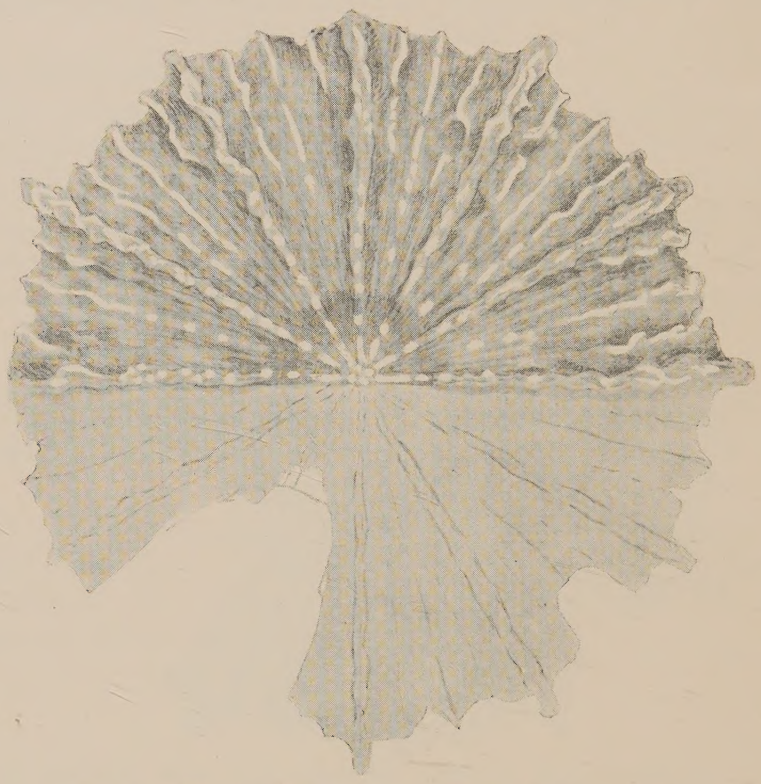

Fig. 2.—*Bathyactis stabilis* n. sp. Lower surface. × 10.

Bathyactis stephana Alcock.

"Investigator" Rep., 28, iii, 5 (1902).

A single specimen 34 mm. from off Natal belongs here. It was sent by the late Prof. Gilchrist and shows clearly the characters described by Alcock.

Genus *Pachyseris* Ed. & H.

Two dead fragments from St. 125, 805 m., lt. br. m. over gy. cl., are not specifically identifiable.

Genus *Psammocora* (Dana).

Gardiner, Proc. Zool. Soc., 1898, 533, and Fauna Geogr. Maldives and Laccadives, 950 (1906).

We experience the same difficulties in respect to this genus as one of us felt forty-one years ago, but, even after this lapse of time, there are few additonal study specimens in our

Museums. Accordingly, we leave the question of the genus, as it would be impertinent to reconsider views on the study of a series of a single species such as follows. The importance of the collector recording not merely the locality and depth, but also such features in the local environment as current flow or protection from same, wave effect, turbidity of water, crowding by other organisms, free-living on rocky, muddy or sandy bottoms, etc., is very clear.

Here, having knowledge of some of these features, we believe that the specimens below enjoyed a somewhat placid existence on a rather smooth bottom, largely free from sand, whereas the type-forms of the species lived on the surface of a lagoon shoal, were subject to changes of temperature, harassed by waves and swept by currents, while on every side other corals, alcyonaceans and algæ, like *Halimeda*, were struggling for their sites.

Psammocora superficialis Gardiner.

Proc. Zool. Soc., 1898, 537, xlv, 2 ; Yabe, Sugiyama and Eguchi, Sci. Rep. Tôhoku Univ., 1936, xli, 4, 5.

There are upwards of 50 specimens which came from St. 45 in the Gulf of Aden, 38 m. deep. " The dredging was a relatively rich one, containing some Alcyonaria, several sponges, etc., also much *Lithothamnion*, some free some attached." The area seems to have been " one of an essentially calcareous-secreting fauna ", the only other corals being a few small *Caryophyllia*. The bottom was " a very smooth one " in spite of the above, certainly neither crowded nor subject to a strong rush of waters.

The coralla are mostly rather flat and spreading, their edges thin, with an imperforate wall below and marked by thin " costal " ridges. A common size is 3–5 cm. across, the whole more or less rounded. The polyp larvæ would appear to have settled on some hard object, budded off polyps and grown out horizontally on all sides, the resulting coralla being slightly domed, as the corallum is formed evenly and continuously below the polyp-layer. Then worms and other boring forms entered the thickened corallum, riddling it underneath with their tubes and giving this part a decayed appearance, the unaltered corallum above seldom more than 10 mm. thick. The slightly lower, surrounding edges of the coralla tend to be killed, but the polyps within usually compensated by growing out new edges at a higher level* ; in consequence the domed growth is less apparent.

Meantime, with the decay below the centre, much of the dead corallum disappears and there results a series of rounded, rather flattened coralla lying freely upon the bottom, their surfaces covered completely by polyps. There is no arrangement of calices with collines between, the whole being smooth and regular.

The calices in surface view average almost 3 mm. across and are shown admirably in Yabe's fig. 5. Superficially the living surface of a corallum may be nearly level, the centres of the calices indicated by tiny pits. More often the calices are 5-sided, shallow areas, marked off by low walls. Relatively even-sided, thick septa with narrow inter-septal spaces cross these, their edges capped by even-sized, transversely-arranged, coarse granules. In young calices there are frequently 6 septa reaching to the columella-space, but in older this number is often more than doubled. It is all a question of filling such

* Such killing might be occasioned by sand or mud, by growths of surrounding organisms or even by rocking on a relatively hard bottom. Growths of Polyzoa, hydroids, worms, *Polytrema*, etc., are found on the undersurfaces, but, by analogy with other species, we are inclined to suggest the last killing agency above.

spaces as become available in the growing calice with septa which must be of approximately similar thickness and structure. Thus, great irregularity prevails in the septal arrangement, as buds may form anywhere over the septa, and the latter always become joined to those of neighbouring calices. A false appearance of branching septa is given when the septa are traced between calicular centres, but the primary septa often run from centre to centre unbranched or branched only on one side.

The axial (columellar) space is quite distinct, but seldom more than 3 mm. across. It may have in the centre a single upstanding rod, or 3 or 4 rods irregularly arranged, or a central pillar with 6 rods around, these simulating pali.

Transverse sections of the coralla show nothing more than can be seen in surface view. In longitudinal sections relatively thick walls can be recognized between the calices and joining the connecting septa; septa and walls tend to be solid below, becoming more perforate towards the surface of the corallum. The centre of each calice is filled-in by relatively thick trabeculæ from the septal edges, and there are no true columellar rods down the same. In addition there exist across the spaces between the septa the thinnest possible dissepiments, but there is no regularity in the distances apart of these. They seem to run to and across the central part and so must form the limiting factor in the depth of the polyp-covering.

Genus *Stephanophyllia* Michelin.

We have specimens before us of all the three species below from off Natal and of *St. complicata* from Saya de Malha, 125–145 fms. These specimens are such as to suggest to us that all three are good species, no undue overlapping. The genus has a wide range into the waters of the Phillipines and Japan. Yabe and Eguchi* refer to 5 living and 11 fossil species from the Upper Cretaceous or later. Of the living species *St. fungulus* below occurs in the Pliocene of Japan. Van der Horst shows that *St. superstes* Ortmann is a synonym of *complicata*.† The fifth species is *S. neglecta* Boschma from "Siboga" Expedition (p. 16, 1923).

Stephanophyllia formosissima Moseley.

"Challenger" Rep., 201, iv, xiii, xvi, (1881).

St. 113, 253 m., s. m. pt., 1 recently dead, 13 mm. diameter.

Stephanophyllia complicata Moseley.

"Challenger" Rep., 198, iv, xiii (1881).

St. 153, 256 m., 3 of 19, 17 and 15 mm. diameter.

Stephanophyllia fungulus Alcock.

"Siboga" Exp., 40, v, 35 (1902); Tijd. Ned. Dier. Ver. (2) VII, 3 (1902).

St. 149, 236 m., cr. r. lth., 1 of 9 mm. diameter.

* 'Sci. Rep. Tôhoku Univ., Geol.' XV, 55–63, viii and ix (1932).

† 'Trans. Linn. Soc.' XIX, 51 (1926) and Ortmann, 'Zool. Jahr. Abt. Syst.' III (1888).

The specimen fits Alcock's description in every respect except that the columella is more diffuse and a little larger. The teeth on the septa are thick, tranverse extensions across the upper edges of the relatively thick septa and give an appearance of broken concentric circles when the upper surface of the disc is examined.

Genus *Dendrophyllia* (de Blainville) Ed. & H.

In our identifications of the species below we have largely followed van der Horst, " Siboga " Rep., 48–58 (1922), ' Trans. Linn. Soc.' XIX, 43–48 (1926) and ' Fish Mar. Survey, S. Africa,' V (1927). We have before us the specimens considered in the last two of these reports, and of *D. japonica* Rehberg from the ' " Terra Nova " Report ', 127 (1929). We also have co-types of Pourtalès' species. An examination of the specimens in the British Museum not having proved at all helpful in a critical direction, our determinations below may be regarded as following the lines of van der Horst to the extent of almost forming a sequel to his three Reports. We agree with him as to the difficulty of separating young forms of *Dendrophyllia* with single calices from *Balanophyllia*, his phrase being " practically impossible ". Furthermore, the latter genus introduces a complication in that young coralla tend to settle on the sides of older and form masses, such anomalies as those referred to by us in *Paracyathus conceptus* (' " Murray " Exp.', 181–186, 1938).

In the present position of the taxonomy of the genus, there are more than 45 living " species ". Of these, we prophesy, that only a fraction will be preserved when the genus is revised by some experienced specialist who has the means to visit the types and who has large collections at his disposal. Even the most upright growing species may become almost a ground mass, its branches fusing together—the polyps share in this fusion—and its calices reduced in size. An example of this is *D. micranthus* (Ehrb.), the most abundant, coral-reef species down at 20 fathoms and deeper; of this, branches of more than a foot long are common, themselves freely branching.*

Dendrophyllia robusta (Bourne).

Lobopsammia robusta Bourne, Trans. Roy. Soc., Suppl., XIX, 212, ii, 10 (1905).
Dendrophyllia coccinea van der Horst, " Siboga " Rep., 55, viii, 21 (1922).
Dendrophyllia klunzingeri van der Horst, Trans. Linn. Soc. XIX, 46 (1926).

St. 45, 38 m., lith., 2 specimens with 14 and 9 calices.

One of us (J. S. G.) had occasion to examine and discuss the type specimen of this species with Bourne, finding himself in disagreement, for he considered that there was no justification for the view that the colony was formed by fissiparity, as indeed is confirmed by Bourne's fig. 10; in this van der Horst agrees. Our largest calice measures 17 by 13 mm., but the average larger calice is about 13 by 10 mm.

Dendrophyllia axifuga Ed. & H. (Text-fig. 3.)

Ann. Sci. Nat., ser. 2, X, 101; Cor. III, 119 (1860).
Van der Horst, " Siboga " Exp., 53, vii, 1 (1922).
Duncanopsammia axifuga Wells, Ann. Mag. Nat. Hist., ser. 10, XVIII, 546 (1936).

We mention here a remarkable specimen lent to us by Dr. Stelfox out of the National Museum of Ireland. It is recorded as coming from Australia and it grew on a clear-lip

* *Vide* van der Horst, ' Trans. Linn. Soc.' XIX, 43 (1926).

pearl shell of 19 cm. diameter. It has a central stem about 7·5 cm. across and from this radiate 12 horizontal branches at a level of 5 to 6 cm. above the shell, each 7 to 9 cm. long and usually dichotomously branching so as to fill all available space. These have polyps only on their upper surfaces and budding takes place at the edge of the terminal calices of the branches. In addition there are two branches standing up vertically over the central mass for 4 to 5 cm. and then bending to spread horizontally.

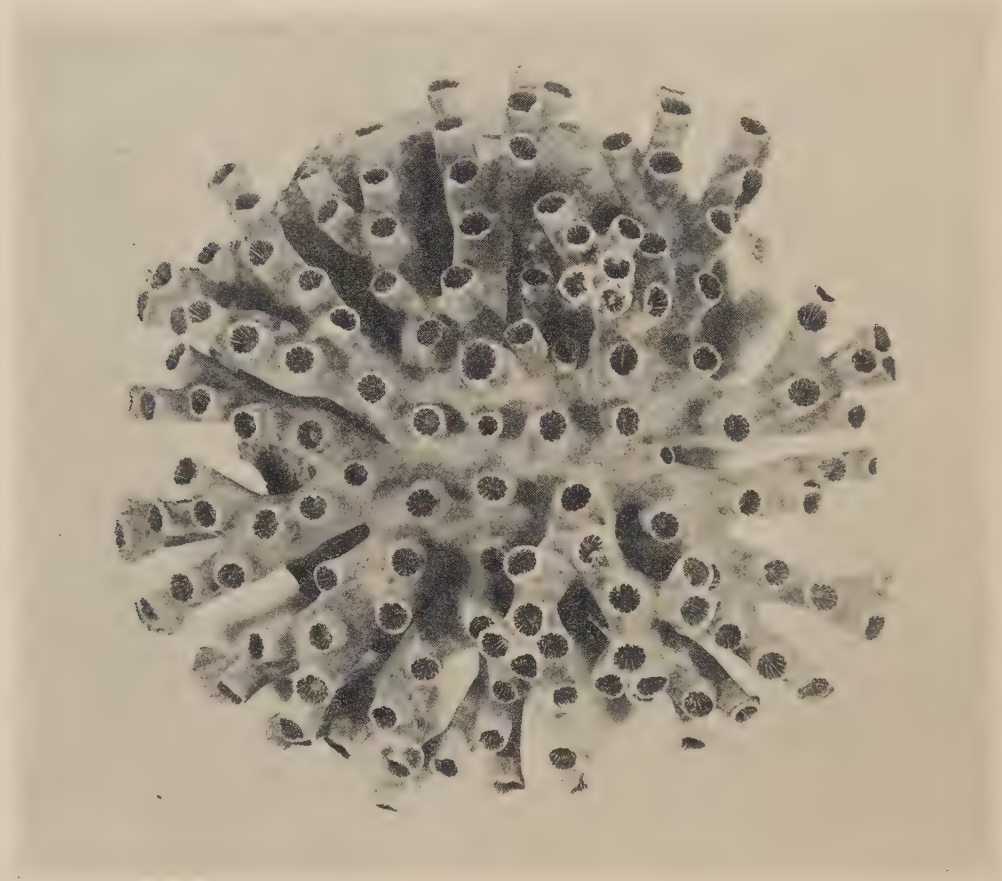

Fig. 3.—*Dendrophyllia axifuga* Ed. & H. × $\frac{2}{5}$. Attached to the outer surface of a pearl shell of 19 cm. diameter.

The specimen displays the natural form of growth of the coral where it is raised above the bottom and uncrowded—and its interest is thus mainly ecological.

Dendrophyllia coccinea (Ehrb.).

Dendrophyllia ehrenbergiana van der Horst, " Siboga " Exp., 55, vii, 3, 4.
Dendrophyllia coccinea van der Horst, Trans. Linn. Soc. XIX, 45, iii, 1–3 (1926).

St. 112, 113 m., cr. r., a specimen 6 cm. high with 3 calices.

St. 157, 229 m., cr. r., a single calice 2·5 cm. high and 2 calices 2 cm. high. This dredging is also remarkable for the large amount of dead coral it contained, all of allied genera. In this could be recognized the above species as well as *D. fistula* Alc., *D. horsti* n. sp. and *Balanophyllia diffusa* H. & P.; it included no imperforate corals.

Dendrophyllia minuscula Bourne.

Trans. Phil. Soc., Suppl., 213, ii, 11 (1905).

St. 157, 229 m., cr. r., the two specimens below.

A branch, 4·5 cm. long with one twig, has 17 calices arranged alternately on either side of its stems. The whole surface is finely granulated and costæ are only visible close below the calices. The colony originally attached itself to a dead *Caryophyllia*, which its base has overgrown.

A bifurcated terminal twig with 7 calices, which were budded-off alternately but now have twisted to one side of its stem, causing the calices to be rather oval and little raised ; it has equal-sized costæ along its whole length.

Dendrophyllia fistula (Alcock).

Balanophyllia fistula Alcock, " Siboga " Exp., 42, v, 36 (1902).
Thecopsammia fistula Marenzeller, " Pola " Exp., 4, i (1906).

St. 106, 183–194 m., gn. m., a single bent calice arising from a broad base, about 3 cm. high, dead.

St. 157, 229 m., cr. r., about 40 branches varying up to 40 cm. long.

The branches are usually dead below but have 1, 2 or a little group of living calices, the side ones arising at 80° to 90°, generally within 10 cm. of a terminal calice. Some of these appear to be secondarily attached forms, their bases extending round a main stem, but in most there is a continuity in the run of costæ which precludes this idea. The 6 primary septa, with the septa on either side fusing to the same, form 6 groups markedly more exsert and upstanding on the theca. There are 4 cycles of septa, IV fusing to III before the latter runs into the rather large, oval columella, often slightly swollen laterally in the centre and formed of packed ribbons.

Some of our specimens are thicker, more branched and with a less naked appearance than von Marenzeller's figures, and nearly all stems up to about 1 cm. below any living calices are dead, with signs of decay. Two young, recently formed coralla have their calices rather cornute and one of these has signs of an imperfect epitheca.

St. 209, 366 m., gr. tr. m. r., a number of dead fragments.

Dendrophyllia horsti n. sp. (Pl. II, figs. 5, 6.)

St. 157, 229 m., cr. r., about 12 specimens.

There are 8 colonies before us, each having 3 to 5 calices and most show a broad base of former attachment and a very dense corallum. The costæ are usually equal and visible from the base along the stems, but are relatively little marked save near the calices. The septa are rather irregular, 4 cycles, over the theca septa I with its neighbouring pair of IV joined and forming exsert groups. The pairs of IV on either side of III join internally to the ends of same and then run into the columella, which only deep down in the calices is joined by I and II ; in consequence III are the narrowest septa in the calice. The columella is a densely-packed, oval mass of ribbons upstanding in the centre of the calice.

The calices vary up to 10 mm. in diameter, very slightly longer than broad. No colony is more than 5 cm. high. All budding is near the calicular margin.

The species bears resemblances in the detail of its calices to *D. arbuscula* van der Horst, ' " Siboga " Exp.' 53, viii, 6 (1922), but his photograph of this species is one of a colony that would be expected to form arborescent growths of some height, whereas our specimens here suggest genetically dwarf, massive, little colonies, never forming high stems or growing vigorously. They tend to be dead at the base and some are bored into by worms.

Dendrophyllia ampheloides Alcock.

" Siboga " Exp., 43, v, 37 (1903).

St. 149, 311–339 m., c. s. sh. cr., a number of dead pieces, which apparently belong to this species, of which Dr. Boschma has supplied us with a good specimen from the Kei Islands, 385 m.

Genus *Balanophyllia* Ed. & H.

We understand the genus as defined by van der Horst.* It is characterized by the coalescence of the septa of higher cycles to form chevrons before running into the columella, which is present in all species. The same remarks apply as to *Dendrophyllia* above and there are about the same number of living " species ".

Balanophyllia cumingii Ed. & H. (Pl. I, fig. 1.)

Ann. Sci. Nat., ser. 3, X, 87 (1847) and Cor. III, 104 (1860).
Bourne, Trans. Roy. Soc., Suppl., 1905, 209, ii, 7, 7*a*.

In 1888 the Cambridge Museum received 16 corals from lat. 6° 01′ N., long 81° 16′ E., 34 fms., which is S.S.E. of Ceylon. All these are horn-shaped, and the larger were lying unattached on the bottom. The longest around the curved side is about 4·5 cm. high, calice 20 by 14 mm., and the rest are rather evenly distributed in size down to 1 cm., 7 by 6 mm. The edge-zone of the polyp overlaps to two-thirds of the height of the corallum, in some of the specimens completely covering the calice. There is no true epitheca, but there may be a certain deposition of lime below the lower limit of the edge-zone, which simulates an epitheca. The costæ and the lines of perforations in the narrow valleys between are distinct. Twelve septa in the larger specimens stand up conspicuously over the theca, but there is great variation here; they have, near the theca, the neighbouring septa fused to them. Ed. & H. and Bourne are both correct for the size of the specimens, and Bourne's figure (7*a*) is admirable. The columella is deeply situated, and the edges of the large 12 septa fall vertically to the same.

In smaller specimens septa I run straight to the columella. Septa II are thinner and extend in at a lower level after having a pair of III fused to its sides; each of the III has similarly 1 or 2 septa of IV joining it. With growth septa II assert themselves more definitely, but there is nearly always a bending of III towards them, though the latter may join direct to the columella, which all the time has been increasing in size and consolidation. Finally, septa V are formed and attach themselves to IV, 38 out of 48 being present in one large calice. Variations occur in that septa may fail to reach the cycle

* ' " Siboga " Exp.' 48 (1922).

to which their edges should fuse. One specimen is a calice regenerated from the broken-off part of the wall of a larger corallite, this including 2 septa of I.

This species bears close resemblances to *B. bairdiana* Moseley, of which the British Museum specimens are before us. They are all very markedly compressed. Septa I and II stand up less conspicuously above the theca and join the columella at a lower level in the calice than the intermediate fused septa. The septal arrangements are admirably shown by Moseley, and there is very little variation in the 5 specimens before us, 2 Moseley's* types and 3 Australian Museum from a single locality.

Balanophyllia diffusa (Harrison & Poole). (Pl. I, fig. 3 ; Pl. II, fig. 4.)

Proc. Zool. Soc., 1909, 906, lxxxv, 4.

St. 112, 113 m., cr. r., 31 calices, mostly attached to dead coralla of the same, usually close to old calicular margins, but with 10 living calices suggesting budding before the death of the original calice.

St. 149, 311–339 m., c. s. sh. cr., a dead and partially decayed corallite of large size.

St. 209, 366 m., gr. br. m. r., a large, broken-off, rather compressed, dead corallite.

St. 157, 229 m., cr. r., 16 living calices, as many partially dead, some with still living " buds ", and a quantity of dead and partially decayed material, the character of " budding " well shown.

Here over 60 calices of firm texture, which vary up to 77 mm. in diameter and are attached by strong stems, the diameter of which may average about half of that of the calice. Much or indeed all may be covered by the edge-zone, but there is no trace of epithecal formation. Usually round the edge of the calice and over the theca are 12 upstanding parts, centred in septa I and II, but sometimes these are not visible. The septal and costal arrangement are as described and figured by the authoresses above, but in odd specimens costæ scarcely show and septa V are more distinguished by their absence than presence ; the septal junctions of IV to the rather lower inner ends of III are more regular than shown in their figure. The calicular fossa is said to be shallow, but this depends entirely on whether the calice has assumed a spreading growth or not ; we should describe the average depth as about half the breadth of the calice. Deep specimens may show the edges of the septa falling almost perpendicularly to where they join the columella. The conjoined septa III and IV in one specimen show this part almost like a tooth ; in others there is a slight, transverse broadening and thickening as they pass to the columella, while the " encroachment " of the trabeculæ of the latter may be found in odd systems of any specimen and is not a specific character. The columella is always well developed, but varies very greatly in breadth with the depth of the calice ; its surface may be flat or an upstanding dome. In young forms it is built of very fine anastomosing trabeculæ, but these, with increase in size of the calices, become coarser, and so fused-up that in an extreme case it might be described as an elongated solid mass of corallum joined by septa I, II and III–IV along the centre of the axial fossa.

It appears to us that the type specimens fall within the limits of variation of our collection in spite of the depth of 3–20 fms. whence they came. Our series of forms taken

* ' " Challenger " Rep.', 191, text-fig. and xii, 4, 5 (1885). We have not found the specimen represented in figs. 6 and 7 of pl. xii.

together suggest that a polyp grows up on some solid base, attains average size, then buds off one or more polyps close to the edge of its calice and dies of " senile decay ". The young polyps then repeat the same process, and the dead and living conjoined produce pseudo-colonial formations.

Balanophyllia cornu Moseley.

" Challenger " Rep., 192, text-fig. and xii, 11–15 (1885).

St. 157, 229 m., cr. r., two very markedly cornute specimens, one with a small form attached, measuring 20, 16 and 10 mm. along the calicular mouth. As there are a large number of specimens in the " Discovery " collections further comment is reserved for the report on the same.

Balanophyllia diomedeæ Vaughan.

U.S. Nat. Mus., Bull. 59, 152, xlv, 3–5 (1907).

St. 157, 229 m., cr. r., one example, straight, top 10 mm. alive, 37 mm. long, calice 10 by 8 mm. The chevrons are well marked, and the columella showing the same character as in Vaughan's three specimens, one which also occurs in *Dendrophyllia horsti* n. sp.

Balanophyllia affinis (Semper).

Van der Horst, " Siboga " Exp., 62 (1922), and Trans. Linn. Soc. XIX, 48 (1926).

St. 141, 44 m., c. s. sh. cr., 7 living and 2 dead ; St. 146, 37 m., 4 living (small) and 6 dead.

Balanophyllia serpentina Vaughan. (Pl. I, fig. 2, below.)

U.S. Nat. Mus., Bull. 59, 155, xlvi, 2 and 3 (1907).

St. 43, 83–100 m., a large corallite, 28 mm. high, 10 by 8 mm. calice with, half way down, a large bud 12 mm. outstanding, and lower still a smaller with calice 3 mm., pushing through a mass of worm tubes and *Polytrema*, nearly all covered by living tissue.

St. 152, 609–915 m., gn. s., 3 living specimens, single corallites measuring 26, 19 (stem broken) and 23 mm. high, calices 10 by 8, 15 by 10·5, 11 by 8 mm. in diameter.

The specimens agree in all respects with Vaughan's description save that there are no secondary corallites on those from St. 152 ; we observe in Vaughan's figures that these are situated (one being doubtful) below the polyp's edge-zone and hence on the dead stems. The texture of the corallum is much lighter than in any other species we have seen, and the thecal wall in places looks like a network of trabeculæ. While there are no true costæ, there may be ridges extending down for a few mm. in correspondence with the larger septa. Odd septa of V are found only in the largest calice.

Balanophyllia præcipua n. sp. (Pl. I, fig. 2, above.)

St. 111, 73–165 m., ? r., three specimens : (*a*) 17 mm. long, greatest diameter 3 mm., terminal and 3 smaller side calices, standing out nearly at right angles ; (*b*) stem 14 mm. (broken end) with 2 calices at right angle, 6 and 10 mm. long, last carrying a short, smaller

calice, diameter 2·5 mm. ; (*c*) stem 23 mm. long with a calice at each end and a smaller at right angles, diameter 3 mm. Total 10 calices.

Shape as described above, only perforate near calice. Wall granular ; costæ corresponding to 12 septa, thin ridges for most of the length of the coralla. Septa relatively thick and rough ; 6 primary, scarcely exsert, extending straight into the columella, often at a lower level than the next. Six septa II each joined by 2 septa of III rather near their columella end and then extending as broad bands into the same. Septa IV only present in a very few systems of the largest calices thus : a pair quite free on either side of septum II ; a similar pair bent outwards from the same and fused to septa of III ; and in one system a free septum interpolated between III and IV. Columella a rather deep trabecular mass with an appearance as if formed by the continuations of the fused chevrons of II and III.

In (*b*) above the structure of the broken end is so perfect as to suggest that polyp-tissues were present here between all the septa. In (*c*) the small end has 6 systems of septa, each consisting of a primary, a secondary and 2 tertiary, the last three forming a chevron, and the large end agrees, while the bud (diameter 1·5 mm.) has one system irregular. This presence of a polyp at each end of the stem recalls the analogous case of *Stenocyathus* Pourtalès.* We presume that in each case the stem has broken and the contained tissues have regenerated polyps.

The species has no close ally. Its form of growth causes us to think of the quite large *Dendrophyllia cornucopia* Pourtalès,† but it is impossible that it can be a young form of any known *Dendrophyllia*.

Genus *Rhizopsammia*.

Rhizopsammia (*?*) *minuta* van der Horst.

" Siboga " Exp., 65, vii, 9 and 10 (1922).

St. 112, 113 m., cr. r., 1 specimen with 3 calices, two of which have just separated from one another, apparently by division of a polyp.

Genus *Endopachys* (Lonsdale).

Endopachys grayi Ed. & H.

St. 90, 91 m., s. sh. cr., a single medium-sized specimen, showing scar of former adherence.

Genus *Heteropsammia* Ed. & H.

The two species below are the same as those so identified by van der Horst from the " Siboga " and " Sealark " Expeditions (' " Siboga " Exp.', 66, 1922, and ' Trans. Linn. Soc.' XIX, 51, 1926) with some of which they have been compared. The species appear to live down to 200 m., with a preference for depths less than half this.

Heteropsammia michelini Ed. & H.

St. 106, 183–194 m., gn. m., several dead specimens, many showing 2 calices.

* ' Cat. Mus. Comp. Zool.' 9 (1871) ; also ' John Murray Exp.', 172 (1938).

† ' Cat. Mus. Comp. Zool.' 45, v, 7 and 8 (1871).

Heteropsammia cochlea Spengler.

St. 72, 75 m., c. s. sh., 3 of 9, 10 and 13 mm., diameter.

St. 80, 16–22 m., c. s. sh., 7 of 6 to 12 mm., dead and worn specimens.

The exsert ends of the larger 12 septa are only conspicuous in 2 specimens of St. 80. The rest present a rather flattened appearance, which perhaps a little emphasizes the oval shape of their calices, suggesting to us that *ovalis** and *cochlea* are identical.

Genus *Goniopora*.

Goniopora stokesi Ed. & H.

Ed. & H., Cor., III, 192 (1860).

Goniopora Maldives (4) 4, Bernard, Brit. Mus. Cat., 76 and 89, vii, 6, and xiii, 9 (1903), identified in text as above.

St. 147, 27 m., sft. cm. m., Horsburgh (Goifurfehendu) Atoll, Maldives.

There are 11 corals, the largest being 29 mm. across ; it is the shape of a half sphere and has on the domed surface about 40 calices with new buds near the spreading edge and, when required above, on the corners where 3 or more calices meet. The middle of the underside is bare and in nowise decayed, the edges to a maximum breadth of 7 mm. are covered with a thin sheet of corallum, quite imperforate, the " epitheca ".

The next-sized corallum is 22 mm. in diameter and 9 others give a succession in size down to 8 mm. with 9 calices. None of these specimens show any traces of " epitheca ", their lower sides built of fused trabeculæ, quite sponge-like in texture.

Bernard described his older Maldivan specimens, chosen out of a long series dredged by one of us, as " built up of successive, hemispherical almost columnar, caps fitting imperfectly into one another ". The description is inapt, for the central part, perhaps inches thick, has no epithecal plates one over another, but is a mass of trabeculæ as described above ; some small specimens collected with these have the structure of the 10 small forms. Bernard (p. 90) regarded his Maldivan forms as " probably a well-marked genetic group ", in other words *G. stokesi*.

Clearly there is no true " epitheca ", based on a " primitive epithecal cup " as Bernard expressed it (p. 18), but a later secondary formation. Remembering that these corals are free and unattached, the advantage of a plate of corallum under the edge is obvious, but the desirability of a complete epithecal covering below the young corals, thus protecting their polyp tissues from the comparatively muddy bottom which the species affects would seem to us to be much greater.

Goniopora lagreneii (Ed. & H.).

Rhodarœa (?) lagreneii Ed. & H., Cor. III, 184 (1860).

Goniopora, China Sea (5) 5, Brit. Mus. Cat. Madreporaria, IV, 73, v, 7 and 8, xii, 11 (1903).

St. 27, 37–91 m., s. sh., two ends of branches.

Bernard's corals were from 32, 40 and 42 fms., and our specimens closely agree in all respects. He also assigns to the same with doubt some coralla from the Macclesfield Bank, 40 fms.

* Semper, ' Zeit. Wiss. Zool.' XXII, 266 (1872).

B. THE ECOLOGY OF SOLITARY CORALS

BY

J. STANLEY GARDINER. M.A., F.R.S.

The Formation of the Skeleton—The Characters of Polyps—The Function of the Skeleton and its Use in Taxonomy—The Variation in Skeletal Characters—Discoid Coralla—Cycles of Septa, Pali and Columella—Use of same in Taxonomy—Importance of Growth Stages—Correlations with Environments—Freshwater—Temperature—Water Movements—Rocky and other Bottoms—Free-living Corals—Pressure—Light in Shallow Waters—Colour—Living and Fossil Corals.

The classification of the Madreporaria can only be regarded as in a profoundly unsatisfactory state. In the first place they have a skeleton of carbonate of calcium, the mode of formation of which we do not know, some workers regarding it as lying completely outside the ectoderm and others as formed within the tissues of the polyp.* All that can be said at present is that it is not derived from that of the Alcyonaria, which is essentially spicular, this sub-phylum not having come into existence before the middle tertiary period, whereas the Madreporaria are pre-Cretaceous. Any phylogenetic relationship to the Tetracoralla is admittedly speculative. However, the natural expectation, in all these groups and in the Hydrocorallinæ, would point to similar physiological processes forming the skeleton in all three. It must be emphasized that it is calcium carbonate with a small trace (less than ·2 %) of magnesium carbonate, while in the salts of seawater more than three parts of magnesium are present as compared with one part of calcium. This is in marked contrast to the lime skeleton of algæ, which is formed intracellularly and contains magnesium in large quantity, estimated as carbonate up to 25%.

Many of the families of Madreporaria are ill-defined, genera being bandied about between them by Milne-Edwards and Haime, Duncan and the more compelling of the later taxonomists. They are hopeless, partially because the worker has usually studied only living or only fossil forms, and in neither case has thought about their polyps. There have been described about 1000 genera, of which less than 400 have been substantiated. Of the solitary corals, the earliest in evolution, more than half the genera are fossil.

The basal element is the species and there are few essential functions in solitary corals that must be represented by anatomical characters. No forms have organs of movement or "mouth parts", the more important functions being concerned with carnivorous

* *Cf.* Matthai, 'Proc. Camb. Phil Soc.' XIX, 160 (1918), which contains references up to his date.

Prof. Matthai in a subsequent paper, "Our Reactions to Stimuli in Corals", gave an excellent account of feeding, his observations in 1915 covering 23 species ('Proc. Camb. Phil. Soc.' XIX, 164, 1918).

Prof. C. M. Yonge, whose brilliant series of papers on the physiological processes of coral polyps is well-known ('Gt. Barrier Reef Reports,' I), in a letter remarks: "Skeleton formation is one of the crucial facts in the evolution and success of the Madreporaria and, it seems to me, is *the* great problem in this group, which remains to be tackled."

feeding, reproduction, sensitivity and protection. In the mechanics of most of these there can be little play to produce a great variety of anatomical characters. Tentacles occur over all septa, but they are not always existent; however, in all solitary corals which we have seen in the flesh they seem to be present. They are introvertible, but sometimes there is a sphincter contractility external to the tentacles, which helps the drawing-in of the oral disc. They are set with nematocysts, sometimes evenly distributed, but more often massed in batteries, either large and terminal, or small and scattered. A second class of nematocyst is found in the mesenteral filaments and stomodæum. Cilia may be present all over the ectoderm, except immediately over the corallum, but are concentrated on the oral disc, stomodæum and mesenterial filaments; their uses, viz. to carry off detritus dangerous to the polyps and to produce food-currents, do not lead to varied anatomical characters. Reproductive organs are situated in the middle lamina* (mesoglœa) of mesenteries and may be male, female or hermaphrodite (usually protandrous) and their products are shed into the cœlenteron; were the polyps of all genera studied, it is possible that they might be found in some genera to be confined to particular mesenteries. The tentacles are extraordinarily sensitive; otherwise there are no special organs concerned with the world around the polyp, and so far as we know all functions of this nature are similarly limited in all corals. The same is perhaps true of the essential functions of the stomodæa and mesenteries. The latter always bear a fixed relationship to the septa, which may be all intermesenterial, or have their last-formed cycle extramesenterial. The stomodæum may have one groove at one end, or one at either end, or a groove between each pair of mesenteries, the coupling of which, together with the differentiation of those attached to the stomodæum, may be of taxonomic value. The presence or absence of directive mesenteries is important.†

The examination of polyps is a laborious business, entailing the use of all the powers of the microscope and varied methods of staining. Sections show little differences in the fine structure of the skeleton, so that a large collection of a species may be examined in a few hours or days, whereas each individual polyp will certainly require weeks, perhaps months. Unfortunately the polyps of most genera of solitary living corals have not yet been examined; most of these grow at considerable depths and their tissues are often irretrievably damaged when brought to the surface in dredge or trawl.

For defence, when the polyp is contracted, the nematocysts of the tentacles can scarcely be everted. Their function is rather concerned with obtaining their carnivorous food, though of course they may serve as a deterrent to the few crawling and swimming animals that attack corals. They are thrown out at the least touch, but only those of the

* *Vide* ' Quart. Journ. Micro. Sci.' LXVII, 101–122 (1923).

† Prof. Matthai's work shows the dominance of the mesenterial influences in the budding-off of polyps in colonial forms. Furthermore, considerable complications are found in most of the above parts and some of these are of undoubted taxonomic importance. Matthai (' Trans. Linn. Soc., Zool.', ser. 2, 1914; ' Phil. Trans. Roy. Soc. London ', ser. B, CCXIV, 313–67, 1926; ' Cat. Madreporaria, B. Mus.' VII, 1928, and in other papers) shows the existence of several types of nematocysts, these occurring in the mesenterial filaments, stomodæal walls, massed in tentacles and scattered through the whole of the external ectoderm, but very rarely found in the calicoblastic part. The ridges between the stomodæal grooves present considerable differences. Matthai stresses the importance of the detailed structure of the mesenteries, particularly that of the pleats carrying the musculature.

We observe that Dr. M. E. Thiel classified the Astræacea on these ideas of budding, dividing them into Directivata and Dedirectivata; ' Res. Sci. Ind. Or. Meer.' II, 39 (1932).

hydromedusan *Millepora* are unpleasant to man. Clearly, protection, viz. the safeguarding of the living polyps, must be elsewhere and surely it lies in the withdrawal of the polyp tissues between upstanding septa, which are covered only by the thinnest layer of tissues. However the corallum may be formed, it is actually the main support , its first appearance being in a firm covering (basal plate) for its attachment, this sometimes extending up around its sides as a wall (*cf.* epitheca as in Flabellidæ) ; above all this serves for the first attachment of the middle lamina (mesoglœa) of the polyp. In that the skeleton bears definite relationships to the tentacles, mesenteries and necessarily to the shape of the polyp, it may be held to reflect its anatomical characters sufficiently for use in taxonomic work. Its value is the greater for this purpose in that it has diverse parts (basal plate, epitheca, septa, theca joining the septa, the outer parts of which are termed costæ, pali and columella). Some of these may be absent, all vary in their interrelationships, and each may have diverse characters, thus in marked contrast to the soft parts which *appear* to have much greater uniformity. There must be added here internal trabeculæ, tabulæ, synapticulæ, dissepiments, etc., all designed for strength and support. Finally all parts may be perforated to allow of a closer relationship of the polyp's cavities with one another.

Perhaps under all the circumstances, the skeleton is likely to reflect a sufficient sample of the polyp's anatomy to justify the founding of genera and species upon it—and, of course, it is only upon the coralla that fossil forms can be considered.* The fact is that the skeleton is convenient to the taxonomist, whereas ultimately the greatest importance lies in the living polyps.

These somewhat optimistic views on the use of the skeleton alone for taxonomic purposes require to be qualified and I would refer to Prof. Matthai's summary of the characters employed by systematists for colonial corals up to 1914† : (1) The form of growth of the colony ; (2) the nature of the intercalicinal peritheca ; (3) the flat or arched character of the dissepiments ; (4) the presence or absence of an epitheca ; (5) the character of the theca ; (6) the number of septal cycles and of the septa constituting each cycle ; (7) the nature of the septa ; (8) the presence or absence of paliform lobes and their shape, size and surface characters ; (9) the nature of the costæ ; (10) the nature of the columella. Prof. Matthai was here concerned with Astræidæ, and he adds : " none of these characters were found to have any constant value and therefore the distinctions based on them would appear to be arbitrary," and his subsequent enumerations of anatomical facts culled from the astræids and meandrids amply bear out this statement.

In the solitary corals which we are considering, nos. 2 and 3 are absent and 5 is of small importance. In dead, dredged forms and in fossil forms all characters dependent on the textures, and presence of surface structures tend to be limited by abrasions and chemical actions in the water or mud. The free edges of structures are often defective, so that all that remains is growth-form, presence or absence of epitheca, costæ, theca and pali, number and inter-arrangements of septal cycles and the nature of the columella, if present. The form of growth little affects the essential features of either polyp or calicular

* Here is a criticism of a proposed classification by Wayland Vaughan in the geological phase of his researches, regarded by him as just : " Nous ne ferons qu'une critique, unique mais importante, a cette classification, c'est qu'elle n'a rien de phylogénétique ; les espèces et les genres de tous les temps et de tous les pays y sont melangés, aucun charactère évolutif n'apparent." M. Dollfus in ' Rev. Crit. de Paléozool,' 65–7 (1906).

† ' Trans. Linn. Soc.' XVII, 2 (1914).

structure. Within individual species of upstanding corals may be found broad-columned coralla, conical, cornute attached or free, the latter resulting from a loosening of the basal attachment or more rarely from fission of the narrow base near the same.* The calices may be round, oval or compressed in each of the above shapes ; in the last, the ends of the calice may reach the same level as the sides, or, may be lower, giving an arched appearance from side view (Pl. I–III).†

In contrast to the above forms are a large number of discoid coralla, parallel evolutions scattered, usually as genera, through several families. The theca extends out horizontally from the calicular centre, and the whole skeleton should be covered by the polyp tissues. Most of these discs were at some time attached and later became free, apparently without breakage, but in *Fungia*, as in certain species of the epithecate *Flabellum*,‡ the stalk still containing polyp tissues may break, a form of strobilization ; how far regrowth from the attached part is a regular phenomenon is unknown, but I have seen examples in these two genera. Some *Fungia*, *Fungiacyathus* (Pl. VII, figs, 19, 20) and perhaps other genera, go further in that their discs split from the centre, each part completely regenerating the corallum. In all corals this power of regeneration is an amazing phenomenon, called forth not only by regular autotomy, but by any accidental damage. We have seen it in nearly all simple genera, of which we have large series, and observations suggest that it is a universal power provided that the pieces concerned each contain a pair of mesenteries. The formation reproduced is that of the original polyp and its skeleton, almost invariably without loss or gain of any part (*cf.* also *Tropidocyathus*, Pl. V).

The cycles of septa seem to be always hexameral to start with, but in a few adult species and occasionally in odd specimens, possibly young forms, an octameral symmetry is found. Ten is very rare except during growth, and we know of no case where it is taxonomic in solitary corals.§ Very commonly the 6 septa of cycle II grow equal in all respects to those of cycle I, giving a 12-symmetry. The side septa do not alter their position materially where the mode of growth leads to a compressed form, but septa of size equal to those of I and II form in the gaps produced on either side of the two terminal septa together with pali if these are found in the species. By this means a 16-symmetry results, but in some of the *Caryophyllia* this is a stage passed through in forming the the 24-symmetry (Pl. I). This has 24 systems, each consisting of one of these first-sized septa (I–III) on one side and three others between it and its neighbours, a pair very small on either side of an intermediate. Conspicuous septal teeth are uncommon in solitary corals ; when present they are usually the terminations of growth lines in the septa and these are often further marked by rows of low spines. Pali follow septa in texture and in the number in their cycle with considerable regularity ; there is usually one to each system. The true or "essential" columella is a lime concretion on the basal plate extending up vertically into the polyp's tissues. It is a rod, a plate, or a series of rods ; these rods, often ribbon-like, are joined by trabeculæ from the larger septa. In

* *Caryophyllia* provides good examples ; see corals in the ' John Murray and " Discovery " (in Press) Reports '.

† The references are to plates and text-figures in Vol. V, No. 7, of this same publication and are inserted solely for the convenience of the reader, who may not be acquainted with the genera mentioned.

‡ Figured in ' Marine Invest. in S. Africa,' II, pl. iii, 16, iv, 22–34 (1902). Note also the wing formation, sometimes developing into hollow struts, and the greater development of the latter as seen in fig. 34. Where there are such rootlets the central stem is retained.

§ In colonial corals ten septa are found in *Madracis*.

the absence of a true columella such trabeculæ may fuse to form a false or " parietal " columella. The columellar surface extends up to the level of the calicular rim or is situated even down to half the depth of the calice ; the fineness and number of the rods also vary and we have seen them fused into a large solid mass.

Usually the genera in solitary corals are determined by the presence or absence of any of the above parts by a generalized form of growth and by the character of the columella if present. Species are often determined on details of these, helped by the number and inter-relationships of septa and pali. With a long series of specimens of solitary corals the specific characters emerge, but no single corallum can be regarded as a type. The growth-form of attached species is often likely to be a difficulty, since at times the polyp seems to be able to lay down additional corallum on any pre-existing skeleton, perhaps thickening its theca externally to the extent of completely burying its costæ and internally solidly filling-up its calice.*

An ever present difficulty is the determination of the adult size of a species—and it is certain that many species have been founded on growth-stages. Unfortunately, the polyp is of little help here, since it may hold its nearly ripe generative products for many weeks. After shedding, regeneration of ova or sperm masses does not take place indefinitely, gaps appearing in any mesentery where they occurred. However, the difficulties in respect to simple corallites are as nothing compared to colonial reef-species whose shapes may be as fluctuating as those of our trees, varying from the types of the Japanese garden of our shops to the same kinds rooted in a protected valley or on an open hillside.

To correlate the different growth-forms attained by coral genera and species with varied environments is as difficult in simple as in colonial corals. In all genera the polyp commences with an upright growth, presumably to raise its mouth above the detritus-layer. It may then become a discoid corallum or remain permanently upright. In the latter any advantage in a cone shape as compared with a broad base can scarcely be conceived, where, as is generally the case, the available space for the polyp tissues within the calice is the same. Often from the same dredging, while most corallites are cones, some happily attached to stone are almost of equal diameter throughout. Freedom, when not genetical, is often a matter of weight ; the cone tumbles and from it a bent horn may be produced by further growth, the mouth bending upwards away from the ground, the whole calicle comfortably rocking if there are any slight currents. Physical abrasion or competition with other sedentary organisms in non-epithecate forms may gradually kill the polyp from its attached base upwards, and then, as it were by a last effort as its edge-zone retreats, the outside of the corallite is overlaid by a fresh deposit of corallum, completely obliterating the costæ. Density of the corallum is often the only means of determining whether this has happened, since the reduction and even absence of costæ is not an uncommon variation. After killing, the exposed corallum is subject to solution, which may remove costæ, but occasionally is found what appears to be a surface deposition of lime from the sea-water. The epitheca lies outside the costæ and, where a theca is

* Any removal of carbon dioxide raises the pH of the water and thus may cause a precipitation of carbonate of calcium (McClendon, ' Carnegie Publ.', 252–8, 1918). The coral skeleton would form the natural nucleus for the deposition of aragonite crystals, should any action of the tissues in their retreat raise the pH. Sections failed to show evidence of such, but the deposition of crystals on crystals would naturally follow the structure of the coral skeleton and no line of demarcation between that formed under the polyp and that deposited from the sea-water might be visible.

present, encloses continuations of the mesenterial spaces of the polyp which continue down between it and the theca, these overlapping its upper edge (*cf. Antillia*). Even in upright corals, normally devoid of epitheca, a thin surface lamina of corallum may often be found, not connected with the basal plate below. This may be developed further in the perforate *Balanophyllia*,* within some species of which all stages may be found from an absence of epitheca to its presence completely covering the corallum almost to the edge of the calice. In the Flabellidæ the epithecate wall may be greatly thickened by an internal deposition of corallum, and any external damage is thus repaired. The epitheca, however, is not nearly so subject to solution or abrasion as any other parts of the coral skeleton that may be exposed to the seawater. Young unattached forms of the colonial *Goniopora*, as dredged, are completely covered by polyp tissues; in further growth an epithecal plate forms where their edges touch the sand or hard mud. As growth proceeds the colony thickens, sinks into the bottom and a series of flat circular rings of epitheca may form above one another, protecting its living edges from the deposits.

To turn to environmental effects, the sea-water everywhere has about the same relative proportions of its chemical salts and hence there can be no effects here, but corals do not appreciate brackish water, seldom continuing to live where there is less than 25% of salts. Heavy rain over four hours of exposure at low tide was never found to kill reef-corals, and the effects of river-flooding seemed to be due rather to sediment than to salinity.

The skeletons of corals are not affected by any ranges of temperature recorded in natural environments so far as can be judged from our knowledge of Gulf Stream, Red Sea and Mediterranean areas. Reef-corals, even when they are attached above low spring levels, are seldom killed by the heatings they receive at low tide, when the water often exceeds 100° F. Cold may have its effects, since there is a tailing-off in genera, species and numbers towards Antarctica, where it is certain that available food shows no decrease.

Water movements are greatest near the surface, and very shallow-living, simple corals have almost invariably a strong column nearly as broad as the calice itself and of little height, to which may be added a tendency to develop the epitheca if present. The common discoid *Fungia* with *Halomitra* and other allied genera are found in depressions and hollows of surface reefs, and owing to their exceptionally massive skeleton are little disturbed, even by the waves.

Strong-columned forms are also characteristic of rocky bottoms, while it is only in still waters that attached cones can persist. The polyp tissues of epithecate corals sometimes overflow their cup. They may thus form hollow rootlets, the calicle continuing to grow vertically. This is common in *Flabellum* (*Rhizotrochus*) and is particularly noticeable in specimens attached to rock. On soft mud nothing lives, but fine deposits are usually smooth on the surface and somewhat hardened below, a quite suitable place for all free forms whatever their shape. Here the perforate *Stephanophyllia* has generally a flat

* This genus has a number of shallow-water species, 7 having been obtained in the Maldives. *B. regularis* makes a habit of growing under rocks or in crevices into low broad columns, seldom more than 5 mm. high; their number is often such as almost to form a society, their depth seldom more than a fathom and often between tide-marks. *B. gemmifera* prefers rather deeper water but still wave-affected; it grows into columns about 20 mm. high, often broadening at the calices. Both of these only produce an epitheca where crowded by other organisms. *B. affinis*, also living in very shallow water on a bottom of sand or mud, is a free conical form, never showing any epitheca. All these species were kept alive; they seemed quite immune to drifting mud.

discoid skeleton, rather heavier than turbinolid discs, and is often found on relatively soft bottoms such as occur in atoll lagoons as well as on ocean banks at 100 to 200 fms. ; its polyp tissues are exceptionally thick and firm and completely cover the skeleton, recalling their condition in *Fungia*. On the same class of bottom *Stephanocyathus* (Pl. VI) starts as an attached form, and grows out into a thin disc, which becomes free. The polyp enlarges, starts to thicken its whole skeleton and to grow out heavy costal spines near its edge. On attaining its adult diameter it grows vertically and the result is a very massive skeleton, its base killed where it has sunken into the deposit below. Of primitively upright growers some show wide, open cones, varying to cup or even saucer shapes, their centres below bedded in the deposit and dead ; loose-lying forms are invariably cornute. The flattened, compressed, cone-shaped *Sphenotrochus* and some other free genera, which remain completely covered by polyp tissues, like this fine sandy bottom ; they are usually well-costulated or covered with low spines and all parts look healthy, no dead patches. A more extreme case is *Tropidocyathus* (Pl. V) which may attain a height of 20 cm., its calice 16 by 11 mm.—88 specimens from one collection were all living without any dead patches, 90% being regenerated individuals from vertically split-up fragments (*cf. Diaseris*-forms of *Fungia*). Both these genera must have lain on their sides, and how they lived at all is a mystery. The perforate *Endopachys* with its flattened cone is found in the same environment but it has side wings which may function to keep it upright ; it also has a complete covering of polyp-tissues and buds frequently form upon its wings. *Heterocyathus** and *Thecopsammia* like this same bottom, the former preferring rather harder ground than the latter ; they are rounded forms of even diameter completely covered by polyp tissues save where the commensal *Aspidosiphon* of their basal parts has its mouth and respiratory openings. They are the only corals with any possibility of movement, and this is no more than a slight burrowing into the surface due to their worms.

Species of *Paracyathus* (Pl. IV), *Balanophyllia* and *Caryophyllia* have also been dredged from the same class of environment ; these are normally attached corals with thick columns. They seem to become detached from the bits of shell or dead coral that form their base and then to lie on their sides. Their polyp is soon killed by the deposit, but it makes a fight by budding-off daughter coralla on its sides, usually near the mouth of the calice. These grow vertically upwards above the deposit and the old dead corallum serves as an attachment ; the whole, as the new corals get heavy again, tumbles over and more buds are formed, so as to produce a simulation of more regular colonial formations. *Desmophyllum* also forms clusters, but its corallites often grow to a great size, their stems correspondingly thickening ; they seem to prefer rocky ground and they could certainly stand up to any current.

It is not conceivable that pressure can have much effect, and, while genera like the discoid *Deltocyathus* (Text-fig. 3, VI, VII, 14 and 16), *Bathyactis* (Text-figs. 1 and 2 above) and *Leptopenus* living normally at some considerable depth, are characterized by delicate coralla, there is no such general phenomenon correlated with depth and there are no examples of fixed columnar forms with similarly thin coralla.

If they can exist in shallow water, solitary corals (*Fungia*, which have symbiotic algæ, excepted) seem to shun the light, and this is also noticeable in the creeping forms

* Forty-three specimens illustrative of the variation of *Heterocyathus æquicostatus* are shown in pl. iii of ' Marine Invest. S. Africa ', III, 1904.

with separated corallites, such as *Cladocora* and *Culicia*. They attach themselves to the undersurfaces of rocks or in crevices and frequently are found living on the sides of reef channels where the scour of the tide is considerable. On reefs the *Cœnopsammia*-forms of *Dendrophyllia* grow into incrusting masses in any crevices below slabs of limestone or dead coral in contrast to the freely-branching and upstanding growths that may be found in most species of the genus living 50 fms. below.* The position is such that we are almost compelled to look to the question of illumination for an explanation of the restriction of so many solitary corals to deep water, all questions of food having failed us after the examination of large numbers of polyps. Perhaps the real position is concerned with the effect of light on the complex of organisms associated with corals in shallow waters. Where there is sufficient illumination there is vigorous algal growth, with its associated fauna of crawling animals, a few swimming forms visitors. Tunicates, Polyzoa, sponges and other sedentary organisms will maintain themselves against plants, even growing over them. Corals never seem to be able to do so, their larvæ preferring the bare glass of submerged bottles and never settling on or maintaining themselves against plants and other sedentary organisms contained in the same bottles.

So far as we know colour is not associated with depth or any other environmental character, forms coloured by symbiotic algæ omitted. We have not enough information, spirit polyps losing their colour except in the case of some browns and blacks, the corallum below always white, except where stained after the death of the polyp. Dredgings show that there is no especial tone correlated with any environment below the light zone (*c.* 50 fms.) and, while most species of a genus bear resemblances in colour to one another, we think of the dense black, brilliant reds and yellows merging into dark browns of such genera as *Dendrophyllia* and *Balanophyllia*, and the tendency to shades of purple in *Flabellum*. Usually the corallum bleaches, but in *Tropidocyathus*, *Sphenophyllia* and *Sphenotrochus* it always retains its brown colour.†

This exposure of our ignorance of corals leads us to plead for light, but could some naturalist tell us how the corallum is formed ? Until this is determined its taxonomic value cannot be duly estimated. While the biologist thinks mainly of the living and the geologist of the dead, cannot they come together ? They find an indissoluble bond in their study of vertebrates and surely there is analogy in madreporarian skeletons, to the hard parts of which the polyp tissues are attached. It may be convenient for museums as storehouses to separate the fossil and living vertebrates, but the taxonomist, who professes to be a specialist solely on the one side, can be deemed only by reason of his historical authority to fall within the scientific fold. There can be no serious difficulty in completely blending the simpler living and fossil Madreporaria, usually small drawer-specimens, and having them examined by the same specialists. This proposal certainly applies to other phyla, as well as to all Actinozoa, but meantime we commend it as a commencement for the consideration of the British Museum, Smithsonian Institute and other similarly great museums.

* No further reference is given to the genus here, nor to *Madrepora* (syn. *Lophohelia*) as the attempts to correlate their growth forms with environment are somewhat speculative. They live at the same depths (also *Oculina*) and their calices are well separated on their stems and represent a form of growth never found in the colonial corals of atoll or other reefs.

† At Porto Praya, Canary Islands, a species of a massive *Dendrophyllia* and one of *Balanophyllia* grow slightly below the low tide level. Both species, determined on their coralla as species, are either red or yellow, forms thus coloured growing alongside each other.

DESCRIPTION OF PLATE I.

Fig. 1.—*Balanophyllia cumingii* Ed. & H. × 1.

Fig. 2.—Above : *Balanophyllia præcipua* n. sp. × 1. (Three coralla.)
Below : *Balanophyllia serpentina* Vaughan. × 1. (Four coralla.)

Fig. 3.—*Balanophyllia diffusa* (Harrison and Poole). × 1.

FIG. 1.

FIG. 2.

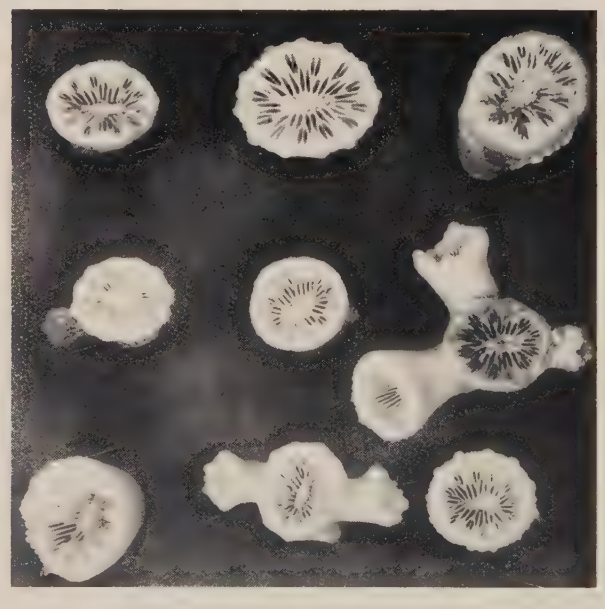

FIG. 3.

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DESCRIPTION OF PLATE II.

FIG. 4.—*Balanophyllia diffusa* (Harrison and Poole). × 1.

FIG. 5.—*Dendrophyllia horsti* n. sp. × 1. Calicular view.

FIG. 6.—*Dendrophyllia horsti* n. sp. × 1. Side view.

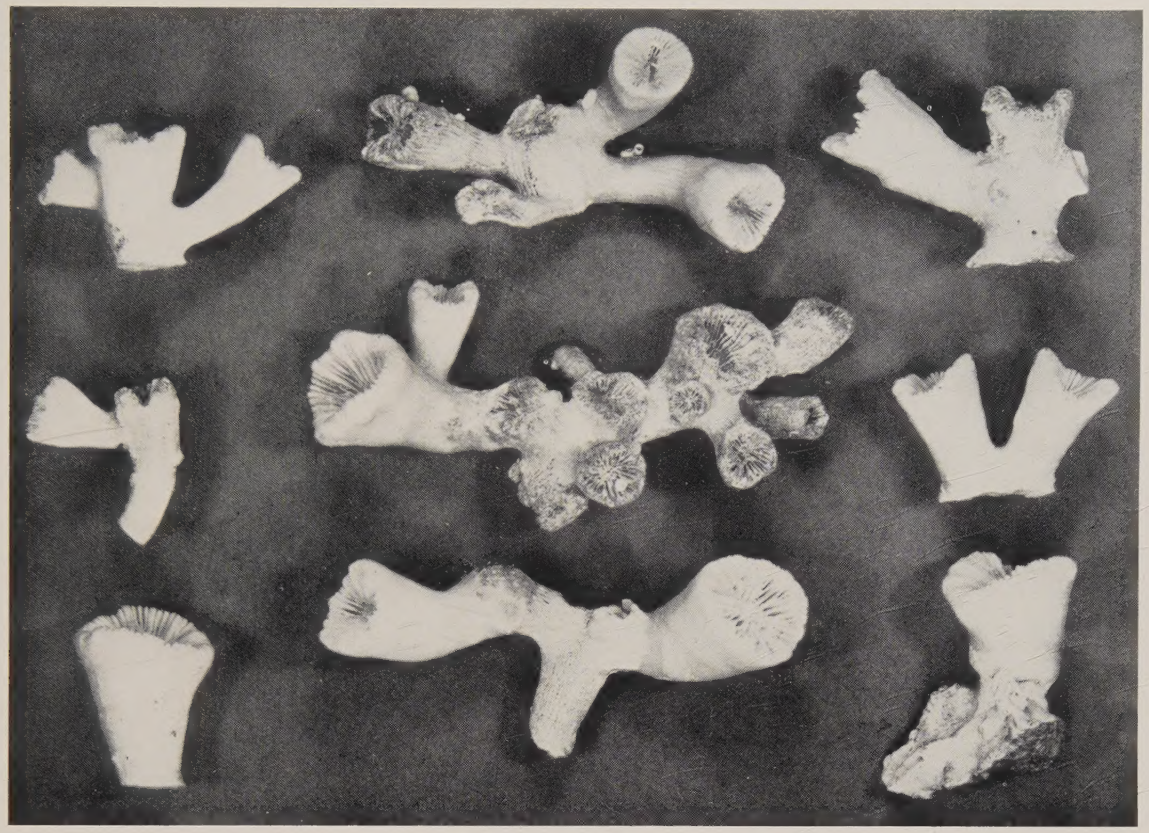

FIG. 4.

FIG. 5.

FIG. 6.

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